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Labial morphology in Blephariceridae (Diptera: Nematocera): a new interpretation with phylogenetic implications, and a note on colocephaly

by

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ABSTRACT

Published studies of mouthparts of adult Blephariceridae have assumed that the labial morphology accords with that of other Diptera, especially that the stem of the labium is constituted by the prementum (theca). The present study shows this assumption to be incorrect: the prementum in this family is present only as a reduced basal component of the labium, and the labial stem is formed by the basal labial palp segments. In the tribes Paltostomatini and Apistomyiini the basal labial palp segments are joined longitudinally and form the main part of the labial stem, with a dorsal channel on the anterior aspect in which the syntrophium reposes, equivalent to the labial gutter normally constituted only by the prementum in other Diptera. Apistomyiini are apomorphically characterised by elongation of the apical labial palp segments into slender tubular forms supported internally by pseudotrachea-like sclerotisations. Monophyly of Paltostomatini is demonstrated by the presence of a small, setose lobe at the base of the inner face of each apical labial palp segment. Fusion of the basal labial palp segments to form the labial stem is a synapomorphy indicating a sister-group relationship between Paltostomatini and Apistomyiini. Evolution of the colocephalous head form in these two tribes is discussed. The condition appears to be associated with obligate autogeny; its adaptive significance may be an advantage gained of abbreviated life of the female flies, which could enhance reproductive success.

INTRODUCTION

The Blephariceridae are an exceptionally interesting family. Evidently with a long history, the flies have evolved a wide range of morphological specialisations from primitive basic forms, and the remarkable immature stages are highly adapted for epilithic, rheophilous life in mountain streams. As a result, there is a large literature on the family, to which many dipterists have contributed. The morphology of the different life stages has been described in considerable detail, and the classification has been progressively developed, now having strong cladistic credentials. Early studies such as those by Edwards (1929), Mannheims (1935) and Alexander (1958) provided landmark reviews, and more recent ones were presented by Zwick (1977) and Courtney (2000).

The present state of blephariceridsystematics derives from the critical cladistic analysis by Zwick (1977). Two monophyletic subfamilies are now recognised: Edwardsininae, comprised by the two relatively primitive genera *Edwardsina* Alexander, 1920 and *Paulianina* Alexander, 1952—and Blephariceridae, constituted by three tribes, the Blepharicerini, Paltostomatini and Apistomyiini, each with a diversity of genera.

The adult mouthparts of Edwardsininae are among the most plesiomorphic known in living Diptera. Tillyard (1922) considered the labium of *Edwardsina* to be '…of primitive Mecopterous form, with separated, two-segmented palps of broad form, with well rounded apices, forming a primitive type of labellum.' Mouthpart forms in

Blephariceridae, derived from a common ancestor shared with Edwardsininae, present a wide range of morphological modifications, with some unique specialisations such as the labellar adaptations for nectarivory in the genera of Apistomyiini (see below).

In the literature, blepharicerid adult labial structure has been interpreted as being constituted in the form typical of Diptera in general. A comparative study of the principal sclerotised components that determine labial form, however, has now shown that this traditional interpretation has in part been incorrect—labial evolution has followed another course in Blephariceridae. This paper presents a reinterpretation of homologies of the components of the adult labium. From this, evidence can be derived regarding blepharicerine tribal relationships, thereby resolving a long-standing systematic problem.

The substance of this study was first presented in poster form, at the Fifth International Congress of Dipterology in Brisbane during October 2002 (Stuckenberg 2002).

MATERIAL AND METHODS

Mouthpart structures were studied using permanent balsam mounts and temporary mounts in glycerol jelly, of dissected specimens macerated in KOH. Figures were made with a Zeiss drawing apparatus on a Zeiss compound microscope, or with a drawing attachment mounted on a WILD stereoscopic microscope. The preparations are in the Natal Museum collection. Representatives of the following taxa were examined: the two genera of Edwardsininae, and their subgenera; all genera of Apistomyiini; all genera currently accepted in Paltostomatini, except the monotypic *Aposonalco* Hogue, 1992, for which good illustrations are available. The many illustrations of heads of species of Blepharicerini available in the literature show mouthpart structures lacking the apomorphies of Paltostomatini and Apistomyiini described below.

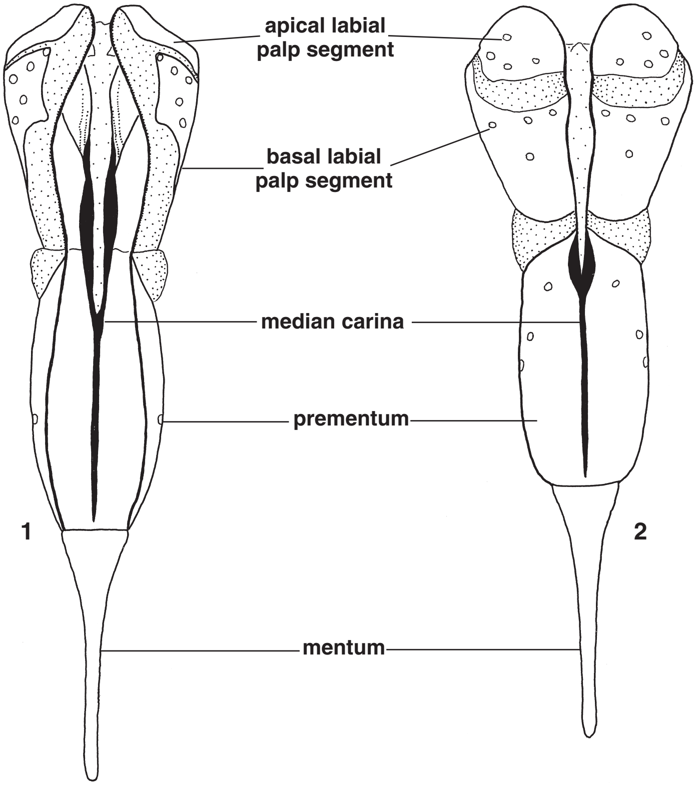
MORPHOLOGICAL TERMINOLOGY

Numerous studies exist on the morphology of mouthparts of Diptera. As a result of differing interpretations of homologies in labial structure, an inconsistent terminology of sclerotised components developed. Snodgrass (1960) noted such inconsistencies in the application of terms based on *mentum*. The following terminology is adopted here and is illustrated in generalised form in Figs 1 and 2.

Syntrophium. This useful term was introduced by Jobling (1976) for the complex of mouthpart components formed collectively by the labrum, mandibles, hypopharynx and maxillary laciniae, which are closely and functionally combined in a morphological entity enclosing the food canal and salivary duct. It has unsuitably been called the 'fascicle' in the literature, a term with several different meanings.

Mentum. 'Postmentum' of Imms (1944). A ventromedian sclerite embedded in membrane below the occipital foramen (Jobling 1928, Crampton 1942). It is retained in only a few nematocerous families, such Blephariceridae (see below), Tanyderidae (Crampton 1942, Fig. 2H), Anisopodidae (Crampton 1942, Fig. 2K), Ceratopogonidae (Jobling 1928), and Psychodidae (Imms 1944, Fig. 11).

Prementum (Crampton 1942; Imms 1944; 'theca' of Jobling 1928). The largest part of the labium, distal and strongly attached to the mentum when this is present; it constitutes the projecting stem of the labium and is commonly termed the 'theca.' It was formed ancestrally by median fusion of the two palpigers. The line of fusion is preserved in a



Figs 1–2. Labium of *Culicoides* species (Ceratopogonidae). 1. Dorsal view. 2. Ventral view, illustrating nomenclature of structural components. (From Jobling 1928)

median longitudinal ridge which is infolded and projects internally as a median carina which forks distally; each branch of the fork is connected to a thickened ventromedian margin of the succeeding basal labial palp segment. In Diptera generally, the prementum is extended longitudinally, and incurved along its anterior surface to form a channel (labial 'gutter') in which the syntrophium normally lies. Presence of the median carina is diagnostic for the prementum.

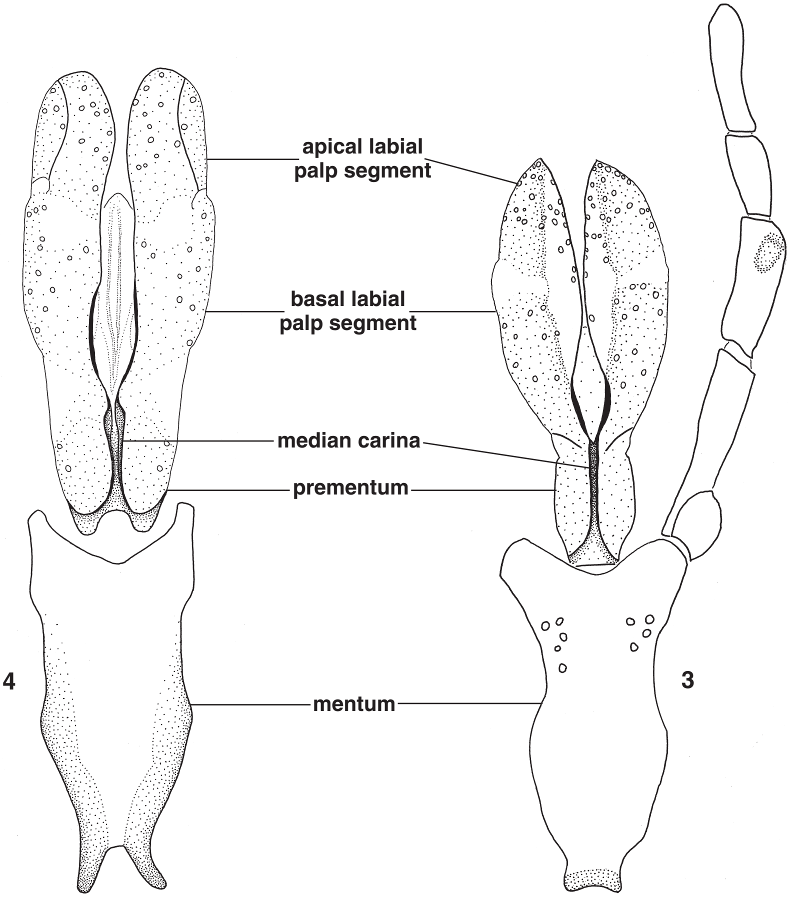
Labella. The paired left and right labella; normally each is formed by modification of the two-segmented labial palp. They are commonly appressed together in the median body plane, and project beyond the apex of the syntrophium. Crampton (1942) termed the first or basal labellar segment as the *basilabellum*, and the second or apical segment as the *distilabellum*, but these terms have not been adopted generally.

Colocephaly. A term introduced by Hogue (1970, 1982) for a distinctive head form that evolved independently in various lineages. Found in both sexes, though not always equally developed, it commonly results in a marked loss of sexual dimorphism, particularly of eye-form. Eyes are reduced, become widely separated, and any upper division of an eye may become vestigial; head wider than deep; antennae often with fewer segments; proboscis very short (usually less than head depth), mandibles absent, maxillary palps may have lost one or more segments, hypopharynx of irregular form and markedly smaller than labrum, suggesting loss of function; basal labial palp segments may be secondarily separated apically or along entire length, apical labial palp segments small and simplified.

LABIAL STRUCTURE IN BLEPHARICERIDAE

Authors appear to have assumed that the blephariceridlabial stem is constituted in the normal way, namely by the prementum (theca), but this proves to be an incorrect homology. Comparative studies show that the prementum is present, but it is only a relatively small basal component of the labium. The stem of the labium is constituted by elongate, longitudinally joined, basal labial palp segments, to which the labella, formed functionally only by the apical labial palp segments, are attached.

Edwardsininae. Tillyard (1922) gave the first description of the mouthparts of *Edwardsina*, but he misinterpreted the Y-shaped apex of the median carina of the prementum to be two 'lobe-like processes'. Tonnoir (1923) corrected Tillyard's



Figs 3–4. Edwardsininae, labium in ventral view. 3. *Paulianina umbra* Stuckenberg. 4. *Edwardsina confusa* Zwick.

description, noting that the 'inner lobes' are a 'furca' of the 'rod-like apodeme' of the theca. Crampton (1942, Figs 1B and 2J) figured the head of a species of *Edwardsina*, showing clearly the mentum, prementum, and basal and apical labial palp segments. Imms (1944, Fig. 7) described the labial musculature in *Edwardsina*; his figure shows the basal segments of the labial palpi to be longer than the prementum, and to be joined by a folded membrane which reaches distally to about the midlength of those basal segments.

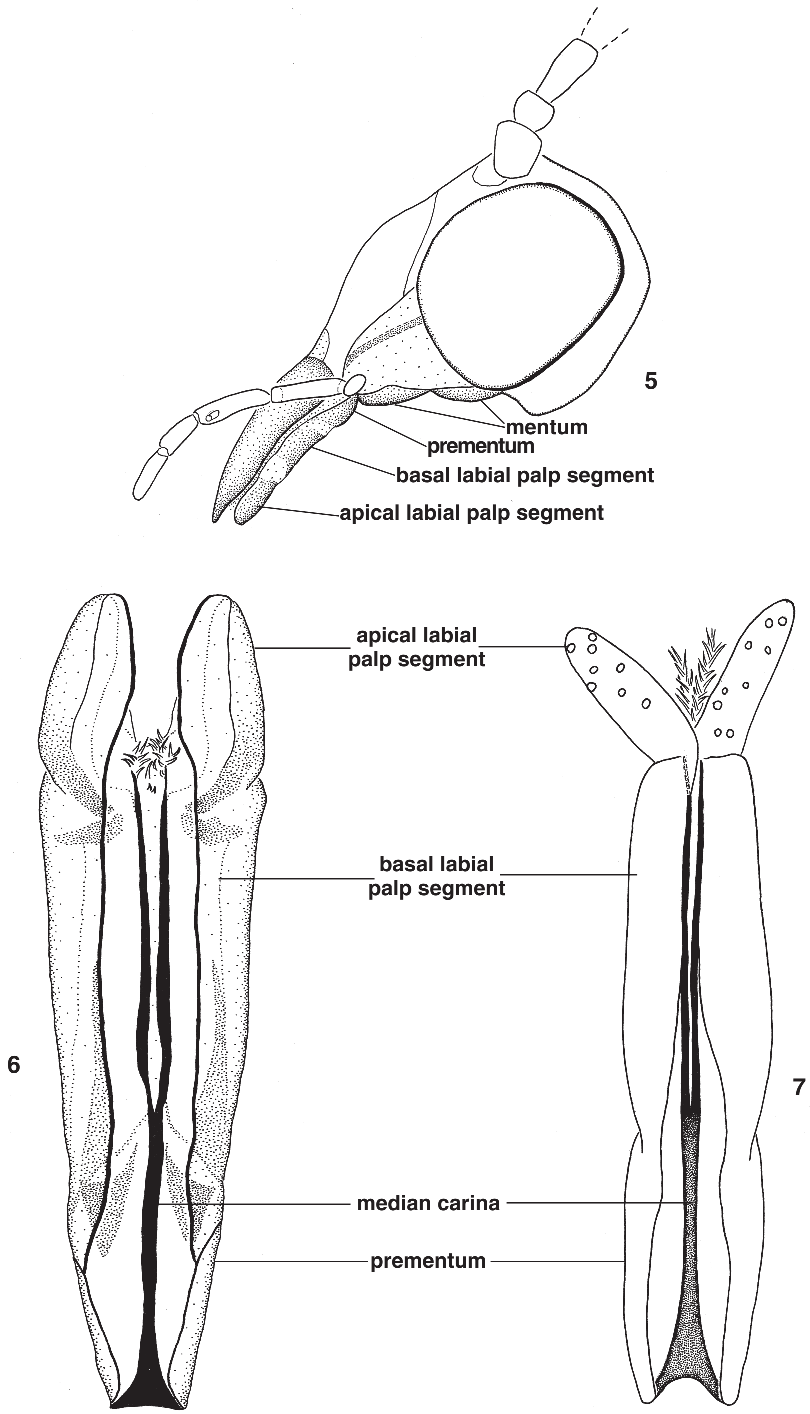
In both genera of Edwardsininae the mouthparts are remarkably primitive (Figs 3, 4). The mentum is large and arched near its middle. The prementum is much smaller, but is identified by the apically forked median carina. The two pairs of labial palp segments are large and not closely joined to one another ventromedially; there is only a short, moderate thickening of the ventromedian edges of the two basal palp segments. Imms (1944, Fig. 7) and Tillyard (1922, Fig. 3) appear to show extensive membrane in *Edwardsina*, between the distal end of the prementum and proximal end of the basal palp segment; this area is clearly shown as membranous by Crampton (1942, Fig. 2J), who also shows membrane ventrally between the basal and apical segments.

Stuckenberg (1958, Figs 10, 11) illustrated the labium in both subgenera of *Paulianina* (*Paulianina s. str.*, and *Eupaulianina* Stuckenberg, 1958). As in *Edwardsina*, the prementum is short, with a strong median carina forking distally; the basal palp segments are widely separated by membrane from the prementum basally, and distally from the apical segments. The two genera have extensive membrane between the lateral margins of the clypeus and mentum. In lateral view (Fig. 5), the syntrophium is seen to slope forwards along the midline of the labium, supported apically mainly between the apical palp segments. The arched form of the mentum is associated with this relationship between the syntrophium and the labial palps.

Crampton (1942, Fig. 2J, posterior view of head of an *Edwardsina* species) illustrated the condition of the labium in Edwardsininae, as being comprised of a small basal prementum bearing the two-segmented labial palps. The basal labial palp segments are more elongate than the apical ones, and form a major component of the labial stem. His interpretation of the morphology agrees with that presented here and by Imms (1944). However, apart from suggesting that this is a relatively primitive labial form, Crampton (1942, pp. 34–35) did not note that such elongation of the basal labial palp segments led to the form of extended labium shown in his Fig. 3D, of the head of a species of *Neocurupira* (Apistomyiini) in anterior view. The extended apical labial palp segments in that figure are labelled simply as 'labella'.

Blephariceriinae – Blepharicerini. Various modified forms which can be derived from the labial states in Edwardsininae occur in most genera of Blepharicerini. See, for example, figures of mouthparts in *Blepharicera* species given by Mannheims (1935) and Hogue (1978).

Blephariceriinae – Paltostomatini. In this tribe the prementum forms only a short basal section of the labium (Figs 6, 7); its identity is confirmed by the presence of the forked median carina. The labium overall has been modified into a straight, quite rigid and narrow structure. Membranous connections between the prementum and basal labial palp segments are reduced, and these segments are strongly joined together in the median plane. The arms of the fork of the median carina firmly unite in overlapping joints with



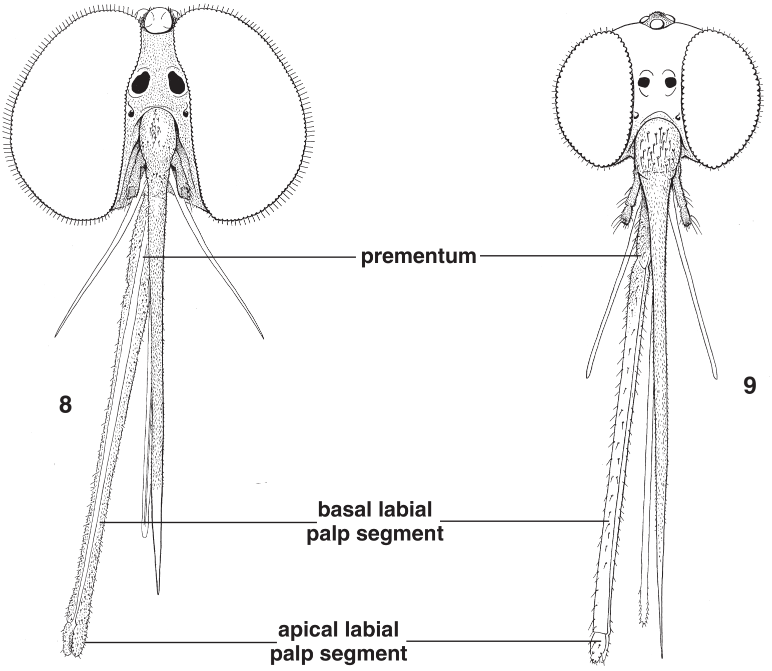
Figs 5–7. 5. Edwardsininae, lateral view of head of *Edwardsina confusa* Zwick. 6–7. Paltostomatini, labium in dorsal view: 6. *Elporia scruposa* Stuckenberg. 7. *Kelloggina elnorae* Edwards.

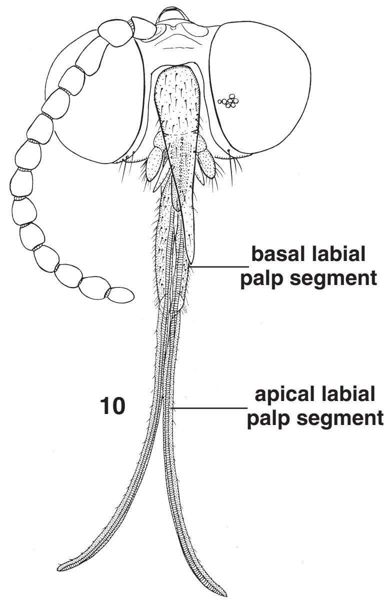
the thickened ventromedian margins of the basal labial palp segments, with which they appear to be continuous. These segments are elongate, forming the stiff stem of the proboscis. They form a channel in which the syntrophium lies, which is functionally the equivalent of the labial gutter of the theca in other Diptera. The short mentum is reduced to a strong but flexible membrane at the extreme base of the labium. Only the apical labial palp segments form the labella (Figs 6, 7). They are closely attached proximally to the ends of the basal palp segments.

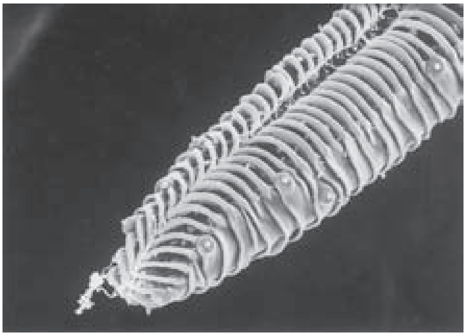
As a consequence of the firm attachments between the prementum and the joined basal labial palp segments, the labium is stiff and adaptable for elongation. In various species of *Paltostoma* Schiner, 1866 for example (Figs 8, 9), the male labium is greatly lengthened through extension of the joined basal labial palp segments. In the South Africa genus *Elporia* Edwards, 1915 several species have a long, slender proboscis through the same modification, but occurring in both sexes (Stuckenberg 1955, Fig. 5A). These extended proboscis forms are surely adaptations for nectarivory. I have observed both sexes of *Elporia natalensis* Stuckenberg, 1955 perched on the flowers of small riparian shrubs, into which their proboscis was inserted. In lineages of Paltostomatini having the colocephalous head form (see discussion of this form below), opposite conditions occur—the labium is greatly shortened, but the small basal prementum with its median carina is usually still preserved, and this head form is clearly secondary. In *Limonicola* Lutz, 1928 the basal labial palp segments have become separated and divergent; the same colocephalous condition characterises the monotypic Mexican genus *Aposonalco*.

Blephariceridae – Apistomyiini. The genera of this tribe, with three exceptions, have the prementum similarly formed as a short basal part of the labium, identified by the median carina. The exceptions are *Apistomyia* Bigot, 1862, *Parapistomyia* Zwick, 1977, and *Hammatorrhina* Loew, 1862; these genera have a relatively enlarged prementum and have lost the median carina, a distinctive synapomorphy suggesting that they constitute a monophylum.The relative size of the prementum in *Apistomyia* can be seen in a lateral view by Kitakami (1937, Fig. 22).

The elongate basal labial palp segments are closely joined medially, and form a narrow, parallel-sided channel in which the syntrophium is tightly held. The distal part of this structure is divided for a short length along the medial axis (e.g. *Apistomyia*) or up to about half of its length (for example *Curupirina* Stuckenberg, 1970). The apical labial palp segments are highly characteristic: they are modified into extended, outwardly-curving, slender, tubular forms, separated over their entire length (Fig. 10). Such mouthparts were described and illustrated by Zwick (1977, 1998), Stuckenberg (1970), and various other authors. In each of the apical labial palp segments, pseudotrachea-like sclerotisations (Fig. 11) have evolved which support the wall of the segment and strengthen its tubular form (Zwick 1998). A narrow, longitudinal slit along the inner surface of each segment gives access to the lumen within that array of sclerotisations. Internally, a slender, tubular duct extends proximally through the basal part of each apical palp segment into the distal ends of the basal palp segments. These two ducts then extend adorally and converge to a level proximal to the apex of the labrum, to the site where the apex of the hypopharynx lies beneath the labrum-epipharynx, this being the location of the distal opening of the food canal. This opening may be close to the distal apex of the labrum, but in some taxa (e.g. *Curupirina* Stuckenberg, 1970) the apex of the hypopharynx is proximal to that.







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Figs 8–11. 8–9. Paltostomatini, male head, frontal view: 8. *Paltostoma rondani* Hogue & Bedoya; 9. *Paltostoma andeana* Hogue & Bedoya; (From Hogue & Bedoya 1989). 10–11. Apistomyiini: 10. *Curupirina kaltenbachi* Stuckenberg, male head in frontal view. 11. *Apistomyia tonnoiri* Zwick, pseudotracheae in terminal portion of apical labial palp segment (SEM image by W. Arens, supplied by P. Zwick).

PHYLOGENETIC CONSIDERATIONS

It has been considered that Paltostomatini and Apistomyiini are related. Edwards (1929) modified the classification of the family by Bezzi (1913) who recognised four subfamilies, uniting Bezzi's Paltostomatinae (originally as Paltostominae) with Apistomyiinae. Such a relationship was queried by Hennig (1973) because no apomorphy had been found that demonstrates Paltostomatini to be monophyletic. Zwick (1981) agreed and concluded that it was uncertain whether Apistomyiini are either a derived subgroup of a paraphyletic Paltostomatini, or are the sister-group of that entire tribe. This matter can now be addressed.

Monophyly of Apistomyiini. This is demonstrated by the specialisations of the labium described above; they have been discussed by Zwick (1977, 1998), who also dealt with larval and pupal characters. Two notable deviations in labial form occur, both the result of secondary modifications: the Australian taxon *Theischingeria rieki* Zwick, 1998 has unusually small imagos, with reduced mouthparts lacking the pseudotracheal sclerotisations of the apical labial segments; and the New Caledonian taxon *Nesocurupira curtirostris* Stuckenberg, 1970 has almost lost the mouthparts through extreme reduction These two species are typically colocephalous (see below).

Monophyly of Paltostomatini. This is demonstrated by the presence of a slender, setose protuberance, possibly a mechanoreceptor, located at the base of the inner face of each apical labial palp segment (Figs 6, 7), and normally present in both sexes. They were first reported by Zwick (1998). I have found them in representative species of most genera of Paltostomatini. They are absent, probably secondarily, in colocephalous taxa, and in the females of *Paltostoma* species which in contrast have mandibulate mouthparts strongly developed, probably for predation.

Fore-leg modifications for probable grasping functions occur extensively in the tribe. These apomorphic developments usually involve the apical tarsomere and claws in the neotropical genera. The claws are well developed, have a comb-like ventral array of spines, and close against the ventral surface of the fifth tarsomere where strong setae are in apposition. Many illustrations of such modifications were provided for *Paltostoma* and *Limonicola* (Hogue & Bedoya 1989; Hogue 1992) and similar modifications are present in many species of *Kelloggina* Williston, 1907 (Lane & d'Andretta 1956; and my observations). In various species of *Elporia* in South Africa, the male has either spinose protuberances, or groups of hook-like setae, or clusters of large, stiff setae, on the ventral surface near the base of the fore tibia or near the apex of the femur (Stuckenberg 1955). *Elporia* species lacking such modifications are mostly colocephalous, notably those of the *capensis*-group. These structures may serve for predation (securing of prey) or for grasping of females for mating. As only the male has such structures in *Elporia*, a sexual role in that genus is probable. A role in predation is possible for the neotropical genera; in *Kelloggina* which has modified tarsal claws, the proboscis is robust and females appear to be mandibulate (my observations of pinned material).

Tribal relationships. Ventromedian fusion of the basal labial palp segments, forming most of the stem of the proboscis, and formation of the main part of the labial trough (gutter) by the joined basal labial palp segments, are synapomorphies of Paltostomatini and Apistomyiini. No intermediate conditions are known in either tribe. On this basis, the tribal relationships within Blephariceridae are postulated to be Blephariceridini + (Paltostomatini + Apistomyiini). Zwick (1977) discussed other adult features, and larval and pupal apomorphies, that could also demonstrate such relationships.

COLOCEPHALY IN PALTOSTOMATINI AND APISTOMYIINI

Hogue (1970, 1982) noted the occurrence of blepharicerid species of neotropical Paltostomatini that share the highly modified head form described above, for which he proposed the term *colocephaly*. Flies with the colocephalous condition tend to have a distinctive appearance due to a disproportionately small head. So far, such species have been described in the genera *Limonicola* (Hogue 1982; Hogue & Bedoya 1989), *Paltostoma* (Hogue & Bedoya 1989), *Aposonalco* and *Elporia* (Edwards 1929; Barnard 1947; Stuckenberg 1955). Colocephaly occurs but is rare in Apistomyiini—the condition has been recorded in *Theischingeria rieki*, and *Nesocurupira curtirostris*. The most significant feature in all these cases is reduction of the mouthparts to the extent that feeding by the flies is no longer possible.

Colocephaly may have developed in association with evolution of the mode of oogenesis known as autogeny. Its essential characteristic is that the adult female fly does not need to feed for ovarian development to proceed to completion. Instead, reserves of nutriments accumulated in the larval fat body are drawn on and are adequate for one ovarian cycle. As the females cannot feed, the condition is categorised as *obligate autogeny*. Oogenesis proceeds during pupation and in the pharate adult. Typically, at eclosion the female fly has the abdomen swollen with fully formed eggs, and copulation probably will soon occur, followed shortly by oviposition and death of the female. That autogeny does occur in these blepharicerids has been confirmed by observations on Australian *Theischingeria rieki* by Zwick (1998) who found fully chorionated eggs in pharate females. Chorionated eggs were present in the pharate holotype of *Nesocurupira curtirostris* from New Caledonia, and some are preserved in the slide-mount. I have seen that females of South African *Elporia flavopicta* Edwards, 1932 and *E. uniradius* Barnard, 1947 are gravid at eclosion.

These evolutionary developments in Blephariceridae parallel those in Simuliidae. In a review of autogeny in Simuliidae, Crosskey (1990) described similarly modified colocephalous forms. He reported the condition to be rare, with only about 2.4% of known species having reduced, non-functional mouthparts. The Simuliidae, however, normally have haematophagous females, and these present a range of autogenous states: *obligate autogeny* (all eggs matured without bloodmeal)—*primiparous autogeny* (first egg batch produced using resources accumulated by larva, subsequent ovarian cycles requiring bloodmeals)—*obligate anautogeny* (a bloodmeal required to mature each separate batch of eggs). There is no evidence that blepharicerids undergo more than one ovarian cycle.

Although predation by mandibulate females was evidently the original lifestyle in blepharicerids, thereby providing proteins for the first ovarian development (obligate anautogeny), no evidence exists that intermediate stages via degrees of primiparous autogeny could have led to obligate autogeny. Transformation in Blephariceridae may have progressed from (1) mandibulate predatory females, to (2) non-mandibulate, nectarivorous females with otherwise fully-formed mouthparts, to (3) colocephalous females with obligate autogeny. Possibly in stages 1 and 2 nutritional resources acquired by larval stages could have increased in importance as more fully obligate autogeny became advantageous.

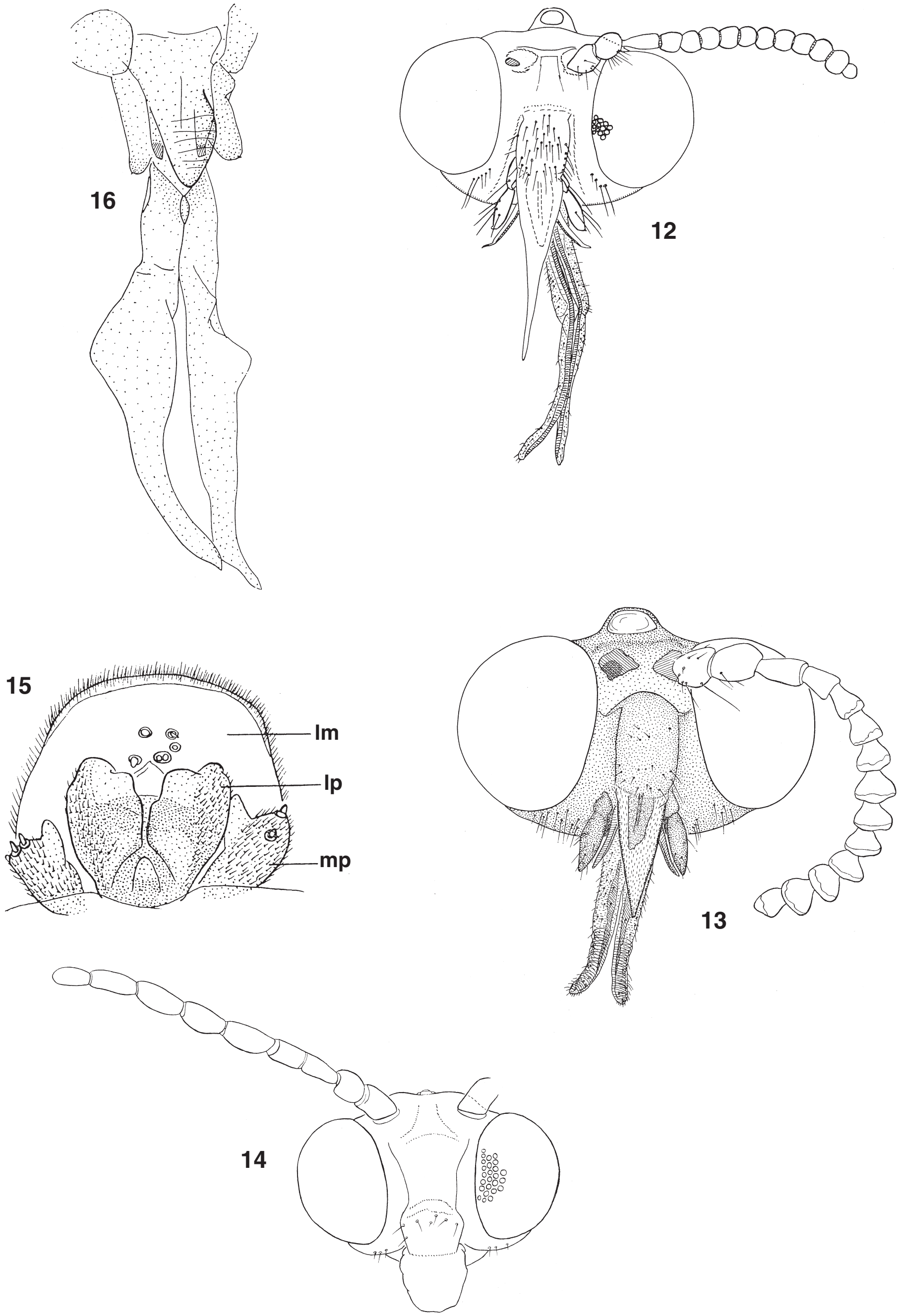
Downes (1971) and Crosskey (1990) considered autogeny in biting flies to be adaptive—enabling species 'to exist beyond the ecological range of normal biting flies.' Colocephalous Simuliidae, for example, occur mostly in extreme environments, such as at high altitudes, or on bleak subantarctic islands, or in high latitudes where summers are brief. Autogeny in blephariceridss, however, seems to have evolved in normally favourable habitats, notably in the tropics and subtropics, so its adaptive value must have another basis.

It seems intuitively anomalous that the adaptations of the adult labium in Paltostomatini and Apistomyiini, especially the latter, should have developed to a high level of specialisation, and then, as it were, abandoned through reduction of the mouthparts to the degree of irreversible incapacity for feeding. The underlying advantages must have had strong selective force. Elongation of the paltostomiine mouthparts, promoted by rigidity of the labium as described above, may have been adaptively advantageous because it facilitated nectarivory; at the same time, the fully-constituted syntrophium could also function in predation. Further modification of the paltostomiine form could have produced the apistomyiine form through elongation of the apical labial palp segments and development of their pseudotracheal supports. As noted by Zwick (1998), observations of feeding by Apistomyiini are difficult to make, and an old record by Schnuse (1901) is still the only definite one. Schnuse observed *Apistomyia elegans* Bigot in Corsica, feeding in composite flowers by spreading the tubular labella sideways, in which position the slit along the inner surface would be ventral within the flower and could draw nectar into the pseudotracheae.

How such an advanced specialisation could be lost is shown by the following remarkable transformation series present in a monophyletic group of New Caledonian Apistomyiini described by Stuckenberg (1970) (Figs 10, 12–16):

- *Curupirina kaltenbachi* (Stuckenberg): (Fig. 10) mouthparts elongate, much longer than head depth, of normal apistomyiine form, apical labial palp segments longer than fused basal ones, with pseudotracheae along entire length.
- *Curupirina microcephala* (Stuckenberg): (Fig. 12, male unknown) mouthparts with normal apistomyiine components, but overall much shorter, labrum longer than fused basal labial palp segments, apical palp segments with well-developed pseudotracheae along entire length.
- *Curupirina starmuhlneri* (Stuckenberg): (Fig. 13) colocephalous condition incipient; labium very short, basal and apical labial palp segments weakly differentiated from each other, pseudotracheae lost, their former presence suggested by transverse wrinkling.
- *Nesocurupira curtirostris* Stuckenberg: (Fig. 14–16) colocephalous condition fully developed; head small, broad, eyes widely separated; mouthparts vestigial, but former presence of elongate apistomyiine labium shown by retention of long, empty pupal sheaths of mouthparts.

The question arises as to why this transformation occurred. This clear progression of stages towards colocephaly—and retention of now functionless mouthpart sheaths in pupae of *curtirostris*—suggests the transformation to have been recent and rapid. It appears that food resources available to the larvae have been sufficiently reliable,



Figs 12–16. Transformation series in New Caledonian Apistomyiini (see also Fig. 10 for unmodified apistomyiine form). 12. *Curupirina microcephala* Stuckenberg; 13. *Curupirina starmuhlneri* Stuckenberg. 14–16. *Nesocurupira curtirostris* Stuckenberg: 14. head in frontal view; 15. posterior view of reduced mouthparts (lm = labrum; lp = labial palp; mp = maxillary palp); 16. empty mouthpart sheaths of pupa; (from Stuckenberg 1970).

abundant and nutritious to favour the modification of ontogeny to include complete oogenesis. Diatoms are the major component of blephariceridlarval diet, and epilithic algae and bacterial colonies are also grazed (Courtney 2000); these have been ancient resources in mountain streams. A plausible explanation could be that abbreviated adult life is selectively advantageous—the flies would be released from the need to obtain protein for oogenesis by predation or other means that require survival, activity and exposure to predators over extended periods.

Finally, a consequence of colocephaly is the problem it may present to the systematist. In itself, the condition is extensively convergent and involves various separate but correlated morphological reductions, thus providing pitfalls for cladistic analysis and determination of relationships. A case in point is the still unnamed Madagascan blepharicerine mentioned several times in the literature as a possible apistomyiine (see Zwick 1998). The species has undergone development of colocephaly to an extreme form, and after long study I am still unable to establish its tribal relationships.

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REFERENCES

ALEXANDER, C. P. 1958. Geographical distribution of the net-winged midges (Blepharoceridae, Diptera). *Proceedings of the Tenth International Congress of Entomology* **1**: 813–828.

BARNARD, K. H. 1947. The Blepharoceridae (Diptera) of the S.W. Cape. *Journal of the Entomological Society of Southern Africa* **10** (1): 3–15.

BEZZI, M. 1913. Blefaroceridi italiani con descrizione di una nuova forma e di due specie esotiche. *Bollettino della Società Entomologica Italiana* **44** (1912): 1–113.

COURTNEY, G. W. 2000. A. 1. Family Blephariceridae, *In*: Papp, L. & Darvas, B., eds, *Contributions to a Manual of Palaearctic Diptera*. Appendix. Budapest: Science Herald, pp. 7–30.

CRAMPTON, G. C. 1942. The external morphology of the Diptera. Part VI. The Diptera or true flies of Connecticut. First Fascicle. *State Geological and Natural History Survey Bulletin* No. **64**: 10–165.

CROSSKEY, R. W. 1990. *The Natural History of Blackflies.* IX+711 pp. Chichester: John Wiley & Sons.

DOWNES, J. A. 1971. The ecology of blood-sucking Diptera: an evolutionary perspective, *In*: Fallis, A. M., ed., *Ecology and physiology of parasites.* London: Adam Hilger Ltd., pp. 232–258.

EDWARDS, F. W. 1929. Fascicle II. Blepharoceridae. *In*: Edwards, F. W., ed., *Diptera of Patagonia and South Chile*, Part II. London: British Museum of Natural History, pp. 33–75, pls.V–VIII.

HENNIG, W. 1973. Ordnung Diptera (Zweiflügler). *Handbuch der Zoologie*. **4** (2). Hälfte (Insecta), zweite Auflage, 2 (Spezielles), Lieferung 20. Berlin: De Gruyter, S. 1–337.

HOGUE, C. L. 1970. Description of a new species of net-winged midge from the Great Basin, with a key to the North American species of the genus *Dioptopsis* (Diptera: Blephariceridae). *Contributions in Science* (Los Angeles County Museum) **178**: 1–10.

——— 1978. The net-winged midges of Eastern North America, with notes on new taxonomic characters in the family Blephariceridae (Diptera). *Contributions in Science* (Natural History Museum of Los Angeles County) **291**: 1–41.

——— 1982. Description of a new species of net-winged midge (Diptera: Blephariceridae) from the Sierra Nevada de Santa Maria, Colombia. *Contributions in Science* (Natural History Museum of Los Angeles County) **340**: 1–10.

——— 1992. A new genus and species of net-winged midge (Diptera: Blephariceridae) from Mexico, with a redescription of *Paltostoma bellardii* Bezzi. *Contributions in Science* (Natural History Museum of Los Angeles County) **435**: 1–12.

Hogue, C. L. & Bedoya-Ortiz, I. 1989. The net-winged midge fauna (Diptera: Blephariceridae) of Antioquia Department, Colombia. *Contributions in Science* (Natural History Museum of Los Angeles County) **413**: 1–57.

Imms, A. D. 1944. On the constitution of the maxillae and labium in Mecoptera and Diptera. *Quarterly Journal of Microscopical Science* **85**: 73–96.

Jobling, B. 1928. The structure of the head and mouth parts in *Culicoides pulicaris* L. (Diptera Nematocera). *Bulletin of Entomological Research* **18**: 211–235, pls. IX-XI.

——— 1976. On the fascicle of blood-sucking Diptera. In addition a description of the maxillary glands in *Phlebotomus papatasi*, together with the musculature of the labium and pulsatory organ of both the latter species and also of some other Diptera. *Journal of Natural History* **10**: 457–461.

Kitakami, S. 1937. Supplementary notes on the Blepharoceridae of Japan. *Memoirs of the College of Science, Kyoto Imperial University* Series B, **12** (2): 115–136, pls I–III.

Lane, J. & d'Andretta, C. 1956. Brazilian Blepharoceridae. (Diptera, Nematocera). *Annals and Magazine of Natural History* Series 12, **9**: 177–204.

Mannheims, B. J. 1935. Beiträge zur Biologie und Morphologie der Blepharoceriden (Dipt.). *Zoologische Forschungen* **2**: 1–115.

Schnuse, C. A. 1901. Bemerkungen über *Apistomyia elegans* Big. (Dipt.). *Zeitschrift für Systematische Hymenopterologie und Dipterologie* **3**: 145–149.

Snodgrass, R. E. 1960. Facts and theories concerning the insect head. *Smithsonian Miscellaneous Collections* **142:** (1): 1–61.

Stuckenberg, B. R. 1955. New Blepharoceridae from South Africa. *Annals of the Natal Museum* **13** (2): 175–209.

——— 1958. Taxonomic and morphological studies on the genus *Paulianina* Alexander (Diptera: Blepharoceridae). *Mémoires de l'Institut Scientifique de Madagascar* Série E, **10**: 97–198.

——— 1970. Ergebnisse der Österreichischen Neukaledonien-Expedition: The Blepharoceridae (Diptera) of New Caledonia. *Annals of the Natal Museum* **20** (2): 217–256.

——— 2002. Labial morphology in Blephariceridae: a new interpretation with phylogenetic implications. *Fifth International Congress of Dipterology*: *Abstracts Volume*, p. 228.

Tillyard, R. J. 1922. Australian Blepharoceridae (Order Diptera). Part 1: Description of new species. *Australian Zoologist* **2**: 159–172, pls XLIV–XLV.

Tonnoir, A. 1923. Australian Blepharoceridae. Part II. Larvae and Pupae. *Australian Zoologist* **3**: 47–59.

Zwick, P. 1977. Australian Blephariceridae (Diptera). *Australian Journal of Zoology*, Supplementary Series **46**: 1–121.

——— 1981. 42. Blephariceridae. *In*: Keast, A., ed., *Ecological biogeography of Australia*. The Hague: Dr W. Junk Publishers, pp. 1185–1193.

——— 1998. Australian net-winged midges of the tribe Apistomyiini (Diptera: Blephariceridae). *Australian Journal of Entomology* **37**: 289–311.